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Buckman, S.S.

Can the sexes in Ammonites be
distinguished?

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CAN THE SEXES IN AMMONITES
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BY S. S. BUCKMAN AND F. A. BATHER.
REPRINTED FROM "NATURAL SCIENCE,"
VOL. IV., JUNE, 1894.

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Can the Sexes in Ammonites be Distinguished?

ALL living Cephalopoda known to us have the sexes separate; no hermaphrodite species has been discovered. It is therefore natural to suppose that the extinct Ammonites were similarly unisexual, some specimens being male, others female. If this be admitted, it becomes of some importance to ascertain whether the difference of sex affected the hard as well as the soft parts of the animal, and, conversely, whether certain differences of form that distinguish individuals may not be of sexual rather than of varietal or specific nature. Clearly it would be wrong to give separate specific names to individuals whose only difference was that of sex.

The opinion that such secondary sexual characters are manifested in Ammonite shells has long been maintained by many eminent authorities, notably among French palæontologists. The first to suggest it seems to have been Ducrotay de Blainville, in his "Prodrome d'une monographie d'Ammonites," Paris, 1840. "Unknown," he said, "though the Ammonite animal be, yet analogy drawn from what we know of the Nautilus does not allow us to doubt that the sexes were separate in different individuals. The females, then, must have had the ventral side more swollen by the ovaries replete with eggs at a certain period. Hence the shell and its aperture must have betrayed these differences by a size and swelling in the former and a relative width in the latter, both greater in female individuals than in those of the male sex, since the semen of the males could never reach such a development as the fertilised ova of the females." De Blainville was followed by d'Orbigny and many other palæontologists. Pierre Reynès, in the Monograph cut short by his untimely death (1879), strongly upholds the distinction of the sexes, saying—"The difference in the dimensions of shells equally ornamented seems to be one of the most convincing proofs. Among individuals, some are slight and of compressed shape, while the whorls of others are broad; we think that the first are the males and the second the females. . . . It results from the comparison of a certain number of individuals of the same species that, without any

doubt, among Ammonites, the compressed forms are almost always accompanied by swollen forms, and that these two forms are constantly associated. The ornamentation and septa are identical; the individuals only differ in the involution and width of their whorls. Anyone making a general study of Ammonites can easily convince himself that the majority of species have two distinct forms, and can prove this whenever the material is sufficiently plentiful. To what cause can this difference of thickness be attributed if not to sex? Ornament is often more pronounced in one sex than in the other, although identical in general arrangement. The ribs and tubercles are then more marked and their number is less; in this case the furrows have a greater depth (*A. bifrons*, *Murchisonæ*, *Martinsii* [sic], *Truelleri*, *Duncani*, etc.). In other species the ornament is in no way changed, the whorls preserve their ordinary proportions, and are not modified in any of their parts."

That differences, not of specific importance, do exist between individual shells, will not be denied by anyone who has studied large collections of Ammonoidea; and these differences may be due to sex, with at least as much probability as to any other cause. The smaller size of the male is certainly paralleled among recent Cephalopoda, e.g., *Sepia*, *Sepiola*, *Loligo*, *Argonauta*. For the views enunciated by Reynès and the other palæontologists mentioned above, something might perhaps be said within small limits; but modern research has done much to disprove them. First, the supposed males and females are found to be not always contemporaneous when the strata are critically examined. Next, the thick and thin forms of a "species" are replaced in modern collections by a great number of forms in all degrees of compression, and these forms do not exhibit that strict agreement in details of ornamentation, etc., which we should expect to find after reading the accounts of these authors. Finally, it has yet to be proved that the thicker forms did actually possess body-chambers of larger capacity than their thinner relatives. It would be so, of course, if the length remained the same; but our investigations rather indicate that the length varies with the degree of compression, so as to maintain, among relatives, the same size of body-chamber in proportion to the whole shell. For instance, in *Stephanoceras* the body-chamber varies in length from about half a whorl in the thick forms (the supposed females) to very nearly two whorls in the thin forms (the supposed males). If the "female" had to enlarge her body-chamber for the accommodation of the eggs, it is obvious that her body-chamber ought to be larger in proportion to the whole shell than is the body-chamber of the "male," who was not called upon to provide this extra house-room.

Recent writers on the subject have therefore gone upon another tack. In their over-anxiety to obey the behest "cherchez la femme!" two well-known French authors have set themselves to prove that the two sexes in the Ammonites differ not only in compression, but in

ornamentation, in shape, in size, in septation, and in the processes at the shell-aperture.

First comes Munier-Chalmas, who, in the *Compte rendu de la Société géologique de France* (no. 14, p. 170, 1892), explains his views on the subject. He considers that the males among Ammonites are represented by certain "scaphitoid" forms, as he calls them, which are distinguished by the following characters:—1. The last whorl is more or less bent back (*réfracté*). 2. The edge of the shell aperture (*péristome*) is furnished with a double process—one auricle on each side—(*apophyse jugale*). 3. The size is relatively small. 4. The evolution of the septa is rapidly arrested.

As types of these *Scaphites*-like Ammonites, Munier-Chalmas indicates the following genera with which we are already acquainted:—*Æcotraustes*, Waagen; *Æcoptychius*, Neumayr; *Sutneria*, Zittel; while he himself adds, as new genera, *Cadomoceras*, of which the type-species is *Ammonites cadomensis*, d'Orb.; *Horioceras*, with type-species *A. baugieri*, d'Orb.; and *Creniceras* which has for type *A. renggeri*, d'Orb. The species belonging to these forms are considered by Munier-Chalmas to be the males of other species, which are females. Thus, *Æcotraustes genicularis*, Waagen, is assigned as male to *Oppelia subradiata* (Sow.); *Horioceras baugieri* (d'Orb.) is made to ally himself with *Distichoceras* (n.g.) *bipartitum* (Zieten); and so on. Why, if these species really are males, generic names, none too happily invented should be given to them, it is not easy to understand. Surely, among Ammonites, as among higher orders of beings, husband and wife should be known by the same name.

This author also treats of the group of Ammonites allied to *A. humphriesianus*, under the name *Cæloceras*. This genus he divides into males, distinguished by an "apophyse jugale," and called *Normannites*; and females, which have no such "apophyse" and are called *Cadomites*. Thus he links the following males and females:—

Cæloceras (*Normannites*) *bigoti* to *C.* (*Cadomites*) *bigoti*.

„ „ *sauzei* to „ „ *polyschides*.

„ „ *braikenridgii* to „ „ *subcoronatum*.

„ „ *linguiferum* to „ „ *daubenyi*.

The example set by Munier-Chalmas has recently been followed by E. Haug, in a paper on "Ammonites des Etages moyennes" (*Bull. Soc. Géol. France*, 3^e ser., t. xx., p. 298). This author has applied the same criteria to the genus *Sonninia*, and has come to the conclusion (p. 300) that the normal *Sonninæ* are the females, and that the group of *Sonninia sulcata*, which contains forms not unlike *Ammonites cycloides*, consists of males. He admits that the species of females far outnumber those of males, but expresses a hope that the missing husbands will eventually be found.

Let us now consider how far these somewhat extreme views, which if true would lead to great complications, are consistent with already known facts.

An objection that might strike even the casual reader of these papers is that all the Lias and much of the Inferior Oolite had been passed through before any of these so-called males appeared ; for the earliest are those which Haug finds among the *Sonninia*. In the Ammonite fauna of the Lias we have as yet only been able to notice one species possessing the characters supposed by Munier-Chalmas and Haug to denote the male sex. That species is *Ammonites accipitris*, J. Buckman, which, as it occurs with *Ammonites oxynotus*, would be considered as the male of that species. Now *Ammonites accipitris* is, unfortunately for this hypothesis, a very rare form, which seems only to have been found in this country, and in one restricted locality. *Ammonites oxynotus*, however, is common enough on the Continent, where it must have lived in a state of single blessedness. But as for the rest of the Liassic Ammonites, where are the males ? Or are we to suppose that the two sexes were exactly alike, and that secondary sexual characters were a comparatively latter-day Jurassic invention ?

Objections such as these suggest the enquiry whether there may not be some other explanation of the appearances that the French authors are so ready to ascribe to sexuality. As that remarkably Heavenly Twin, Angelica Hamilton-Wells, reminds us, "so unwholesomely is the imagination of a man affected by ideas of sex."

Now the characters that Munier-Chalmas has hit upon as "masculine" are in great measure those which appear in the different Ammonite-stocks or lines of descent when they draw near the period of their extinction. They are, to a large extent, characters such as we have learned to associate with the old age of a race, when it is in a sense retrogressive. May we not then suppose that these so-called males are in reality the final expressions of the various races to which they belong ? At all events, *Cadomoceras*, *Æcotraustes*, and *Æcoptychius* seem explicable as such retrogressive forms ; but *Normannites* is admittedly a difficulty.

The sexual hypothesis, however, is one about which it would be foolish to dogmatise ; it deserves full consideration. Munier-Chalmas and Haug say that they have many males yet unfigured ; and this statement is borne out by other collections, so far as the Oolitic rocks are concerned. It must be remembered that our knowledge of the Ammonite fauna is as yet very imperfect, large though the number of described species appears to be. Some of the Jurassic rocks have been done very scant justice to, and their treasures are still unknown to Ammonite literature.

Apart, however, from any special hypothesis, there is one consideration that may profitably be brought to the notice of those who endeavour to discover signs of sex in the extinct Cephalopods. They may be recommended to enquire whether such signs are to be found in the living species of *Nautilus*, and if so, what those signs are. Of course *Nautilus* is not an Ammonite, does not even belong to the same Order of Cephalopoda ; still there can be very little doubt that

the situation of the animal with regard to the shell was much the same in the Ammonites, and that any effect produced in the Ammonite shell by sexual difference would probably also be found in that of *Nautilus*.

Owing to the somewhat curious fact, which may of course be mere coincidence, that the large majority of specimens of *Nautilus* examined by eminent naturalists have been of the female sex, not much has been said upon this subject by zoologists. J. D. Macdonald, however, in his account of the anatomy of *Nautilus umbilicatus* (*Phil. Trans.*, 1855, p. 277), has a sentence which, though its logic is obscure, certainly bears on this question. He writes: "The specimen of *N. umbilicatus* examined proved to be a female, a fact which may serve to modify the views of those who, adopting the ingenious speculations of d'Orbigny with reference to the sexes of the Ammonites as indicated by the characters of their shells, apply them also to the several kinds of *Nautili* known." He appears to be alluding to the belief that the species known as *N. umbilicatus* was nothing more than the male of *N. pompilius*. Still the fact that it was really a true species, though it might upset that particular belief, would not conflict with the idea that there might be some differences between the shells of the two sexes.

An attempt to demonstrate some such difference was made in the same year by J. Van der Hoeven (*Verh. d. kon. Nederl. Akad. van Wetensch.*), who had at last obtained a male *Nautilus pompilius*. After describing various external sexual characters of the animal, he proceeds:—"It seems to me moreover as not improbable that in the shape of the hood there is a sexual distinction, and that this, when of the same average length, is about two centimetres shorter in the male individual. With this is also connected a distinction in the shape of the shell; in the male individual this is broader and more globose at the aperture, more laterally compressed in the female animal. Also the edge of the aperture of the shell in the male animal is, as it seems to me, more strongly sinuous; in the female animal more regular." It will be noted that these points of difference, assuming them to be correct, by no means agree with the suppositions of de Blainville, d'Orbigny and others with regard to Ammonites; and in such a case surely no one will venture to exclaim "So much the worse for the *Nautilus*!" Moreover, if one may judge from the drawings by A. G. Bourne which adorn Professor E. Ray Lankester's article on Mollusca in the "Encyclopædia Britannica," both the male animal and its shell are proportionately broader than the female. It is indeed by no means necessary to suppose, as did the older writers, that the swelling of the female organs involves a widening of the shell. The shell of the body-chamber must necessarily have been formed before the development of the ova, and any pressure caused by the enlargement of the soft parts must act on the soft parts themselves quite as much as on the shell. Since, however, the shell is hard

and unyielding, the obvious result of such pressure is merely to push the animal forward so that it obtains space by lengthening rather than by widening the body-chamber.

Some caution is, however, to be exercised before accepting the views which Van der Hoeven based upon the evidence of a single specimen. Differences such as he points out do certainly exist between *Nautilus* shells; but a careful examination inclines one to regard them as due to difference of age rather than of sex. As *N. pompilius* grows older, the sides of the shell-aperture begin to swell outwards, so that the width of the aperture is greater towards the inner or dorsal region of the whorl; and this produces a sinuosity in the margin, which continues to increase with age up to a certain point. May it not then be that Van der Hoeven was deceived by just the same kind of characters in the individual species as we believe Munier-Chalmas and Haug to have been deceived by in the race?

To sum up the case in language that has often been objected to in this Journal, and with which its readers cannot, therefore, be wholly unfamiliar,—we suggest that the characters in question are auxologic or bioplastic rather than sexual, being in some cases phylo-gerontic, in others merely ephebic or gerontic, and we conclude that sexual dimorphism has yet to be proved for Ammonite-shells.

S. S. BUCKMAN.

F. A. BATHER.

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